

RESOURCE UTILIZATION BY LARVAE OF *PARACANTHA GENTILIS*
(DIPTERA: TEPHTRITIDAE) IN CAPITULA OF
CIRSIIUM CALIFORNICUM AND *C. PROTEANUM* (ASTERACEAE)
IN SOUTHERN CALIFORNIA

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Abstract.—Resource utilization and resource sharing by larvae of *Paracantha gentilis* Hering were analyzed in capitula of two native thistles (Tribe Cynareae): *Cirsium californicum* Gray and *Cirsium proteanum* J. T. Howell. Guilds described and analyzed for thistle-insect systems in Europe, though more complex than in southern California, apparently lack phytophages with the trophic strategy of *P. gentilis*. This tephritid displays rarely solitary, mainly aggregated attack on immature, closed capitula, but unlike European Tephritidae, does not form galls or otherwise cause host-tissue proliferation. Instead, feeding behavior of third instars of *P. gentilis* showed a density-dependent change in feeding niche from ovule-feeding alone to ovule, upper receptacle and plant-sap feeding which extended the range of available resources and minimized intraspecific competition.

The feeding-niche of *P. gentilis* in thistle capitula is novel by European criteria, and exemplifies the failure of phytophage communities to converge in structure despite similar resources on different continents.

Key Words: Insecta, resource utilization, guild structure, Tephritidae, gall-formers, *Cirsium*, evolution, thistles

Resource utilization by thistle-head insects was described by Zwölfer (1985) as "... the percent of flower heads in a sample containing phytophagous insects or showing signs of insect damage." This parameter is more precisely measured as the number of damaged achenes per capitulum (= head). Zwölfer (1985) used resource utilization and guild structure to study the feeding ecology of several thistle-insect systems in Europe.

Ten species of *Cirsium* (Asteraceae, Tribe Cynareae) are native to southern California (Munz 1974). Few native stenophagous insect species are associated with native *Cirsium* spp. in North America (Goeden and Ricker 1986a, b, 1987a, b). In contrast, many stenophagous species are associated with European *Cirsium* spp. (Zwölfer 1965).

This disparity offers opportunity for comparative studies of resource allocation and resource utilization by thistle-head insects.

Paracantha gentilis feeds in capitula of eight species of native *Cirsium* thistles and the introduced *C. vulgare* (Savi) Tenore in southern California (Goeden and Ricker 1986 a, b, 1987a, b) as well as several different species of native *Cirsium* in northern California (Pemberton et al. 1985) and elsewhere in North America (Steck 1984). In *C. californicum* Gray, Goeden and Ricker (1986b) recorded *P. gentilis* as the dominant phytophage reared from 19 (73%) of 26 samples (average 50 capitula/sample). Three other insect species found in less than 50% of the capitula from the same samples were: *Rotruda mucidella* (Ragonot) (Lepidoptera:

Pyralidae), *Platyptilia carduidactyla* (Riley) (Lepidoptera: Pterophoridae), and *Orellia occidentalis* (Snow) (Tephritidae). *Paracantha gentilis* was reported from 62% of samples of *C. proteanum* capitula by Goeden and Ricker (1986b). Among the three other insect associates mentioned above, *R. mucidella* was the dominant phytophage in *C. proteanum* capitula, occurring in 92% of the samples (Goeden and Ricker 1986b).

Zwölfer (1988) outlined three trophic strategies for thistle capitula-infesting insects in Europe: (1) An early-aggregated attack in closed young capitula, usually combined with gall formation, that lead to gregarious feeding behavior and protection from parasitoids and predators. In Europe, these insect associates are highly host-specific Tephritidae, Cynipidae, and Curculionidae. (2) Feeding on the maturing achenes and receptacle without induction of galls. Oviposition takes place in older capitula, only single eggs are deposited, and capitula already occupied usually are avoided, e.g. Tephritidae and Curculionidae in Europe. (3) Polyphagous species that usually occur singly and oviposit after a capitulum has opened. The larvae are highly mobile, aggressive, often cause accidental mortality of other individuals in a capitulum, and are typically the dominant phytophage, e.g. Anobiidae, Pyralidae, and Tortricidae in Europe. Harris (1989) distinguished between ovule (unfertilized) and soft or hard achene (fertilized ovule)-feeding by insects in knapweed and thistle capitula, a modification of Zwölfer's (1988) scheme which we have used in our discussion.

Preliminary field studies by Goeden and Ricker (1986a, b, 1987a, b) suggested differences from European Tephritidae in the way *P. gentilis* feeds and interacts with other insects infesting capitula of native *Cirsium* thistles in southern California. Comparisons were based on two thistle-insect systems involving (1) a *C. californicum* Gray population in which *P. gentilis* was the only capitulum infesting species and (2) a *C. pro-*

teanum J. T. Howell population in which *P. gentilis* was part of a capitulum-infesting guild composed of as many as four species.

MATERIALS AND METHODS

Cirsium californicum capitula were sampled at Mill Creek, San Bernardino National Forest, San Bernardino Co., CA, and *C. proteanum* capitula were sampled on Sawmill Mt., Angeles National Forest, Los Angeles Co., CA. Current season's capitula were collected during the Spring and Summer of 1987, 1988 and 1989. Overwintered heads from 1986 were collected in early Spring, 1987, and stored at 5°C for later dissection.

Serial dissections of capitula at different developmental stages were carried out to determine larval feeding behavior. Dissected eggs and larvae were placed in covered glass petri dishes lined with filter paper and soaked with physiological saline and held in darkened growth chambers at 27°C until identified and then were held for pupariation and adult emergence, or were preserved or discarded.

Field sites consisted of scattered individuals and patchy aggregations of 10–50 thistles growing along roads and on south-facing hillsides. At the Mill Creek site, 25 plants were inspected on each sampling date, and a total of 10–25 capitula were collected on each date for later dissection. The number of capitula on all plants occurring in a 3 × 3 m-area at the Mill Creek site was counted on four occasions during April–May, 1988, to determine phenology and capitulum production. Oviposition by overwintered females in the small immature capitula (commonly and erroneously called “buds”) also was monitored on a weekly basis for the entire season during 1987 and 1988.

Individual larvae and puparia dissected from capitula were placed in 60-ml³ plastic vials fitted at one end with 100-mesh brass screening for ventilation and held in the insectary of the Department of Entomology, University of California, Riverside. Insectary conditions were 26° ± 1°C, 30 to 60%

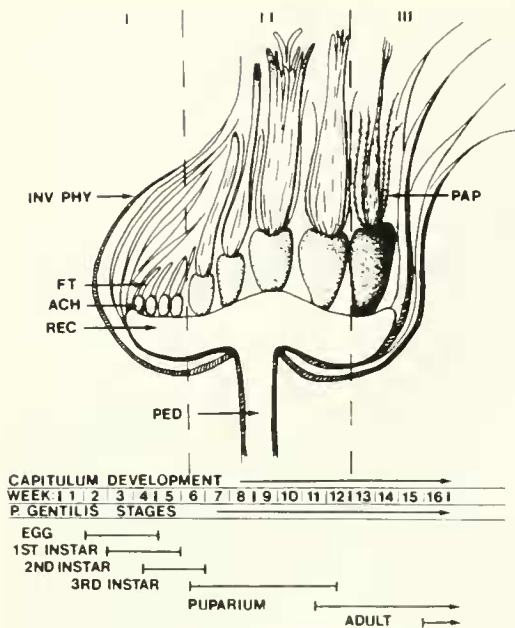


Fig. 1. Phenology of *Paracantha gentilis* in capitula of *C. californicum*. I. Immature capitulum. II. Blossom. III. Post-blossom. ACH, achene; FT, floral tube; INV PHY, involucral phyllaries; PAP, pappus; PED, peduncle; REC, receptacle.

RH, and a 12-12 (l/d) photoperiod. Voucher specimens of all insect species involved are stored in the research collection of RDG, and eventually will be offered to the collection of the Department of Entomology, University of California, Riverside.

RESULTS AND DISCUSSION

Resource utilization.—The phenology of *Paracantha gentilis* in capitula of *C. californicum* in southern California is shown in Fig. 1. *Paracantha gentilis* follows the first trophic strategy in Zwölfer's scheme described above, but with a major difference—although it oviposits in closed young capitula and usually feeds gregariously (up to 12 larvae per capitulum), it induces no galls.

In the present study, resource utilization was calculated as the percentage of attacked capitula in a sample (Table 1). The accuracy of this statistic will be discussed below with regard to feeding strategies of capitulum-

Table 1. Resource utilization or percent of *C. californicum* and *C. proteanum* capitula infested by three phytophagous species.^a

Sample	Capitula Dissected	No. (%)		
		Capitula Attacked		
		P G	R. M.	O. O.
<i>C. californicum</i> ^b				
1986	15	12 (80%)	0	0
1987	110	86 (78)	0	0
1988	30	24 (80)	0	0
1989	40	31 (77)	0	0
Totals	195	153 (78)	0	0
<i>C. proteanum</i> ^c				
1982 ^d	27	18 (66)	20 (74)	21 (78)
1983 ^d	27	8 (30)	17 (62)	11 (41)
1986	30	16 (53)	12 (40)	6 (20)
1987	50	37 (74)	43 (86)	26 (52)
Totals	134	79 (58)	92 (68)	64 (47)

^a P.B., *P. gentilis*; R.M., *R. mucidella*; O.O., *O. occidentalis*.

^b Mill Creek.

^c Sawmill MI.

^d Unpublished data Goeden and Ricker.

infesting Tephritidae. Thus, resource utilization by *P. gentilis* in *C. californicum* was 78%, as 153 of 195 capitula examined were attacked. In *C. proteanum* with its complex insect guild, resource utilization by *P. gentilis* was 58% (79 of 134 capitula), by *R. mucidella* was 68% (92 of 134 capitula), and by *O. occidentalis* was 47% (64 of 134 capitula).

In southern California, *P. gentilis* is an early-aggregated attacker; whereas *O. occidentalis* is a solitary phytophage that oviposits after the capitula begin to open and whose larvae feed on the floral tubes and maturing achenes. Thus *O. occidentalis* employs Zwölfer's second trophic strategy. *Rottruda mucidella* and *P. carduidactyla* follow Zwölfer's third trophic strategy as highly mobile, indiscriminate feeders (Goeden and Ricker 1986b, 1987a, b).

Resource sharing.—Resource sharing by *P. gentilis* larvae in capitula of *C. californicum* involved avoidance of intraspecific competition for food early in their life cycle. Females oviposit eggs singly or in clusters

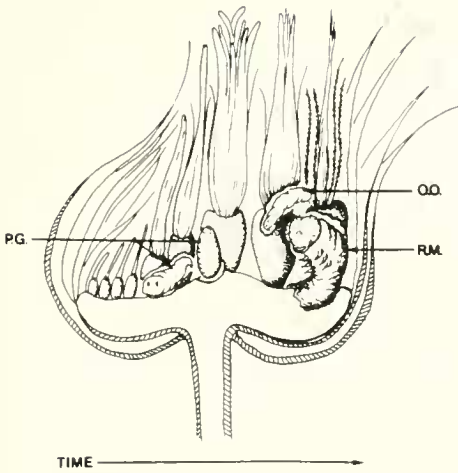


Fig. 2. Temporal and spatial partitioning (diagrammatic) of a thistle capitulum by three of the most common insect species comprising a complete guild in southern California. P.G., *P. gentilis*; O.O., *O. occidentalis*; R.M., *R. mucidella*.

of up to 13 centrally in the capitula (Headrick and Goeden 1990 and unpublished data). After eclosion, first instars tunnel into separate, nearby floral tubes where they feed for the entire stadium. Second instars leave these initially attacked floral tubes and tunnel towards the outer margin of the capitula through a series of floral tubes well above the level of the achenes. Thus, central placement of the eggs and differences in feeding modes between the first two instars minimized competition between these instars in capitula of *C. californicum*. Third instar feeding was confined to the central ovules, and as noted below, scored the upper receptacle at higher larval densities despite the presence of an outer ring of uneaten ovules remaining in the capitulum.

Interspecific competition in *C. proteanum* was avoided among guild members by temporal and spatial division of the capitula resources (Fig. 2). *Paracantha gentilis* avoided substantial interspecific competition because it attacked early and fed and pupariated centrally at anthesis surrounded by a mixture of dried feces and fragments of floral tubes and pappus hairs. This type

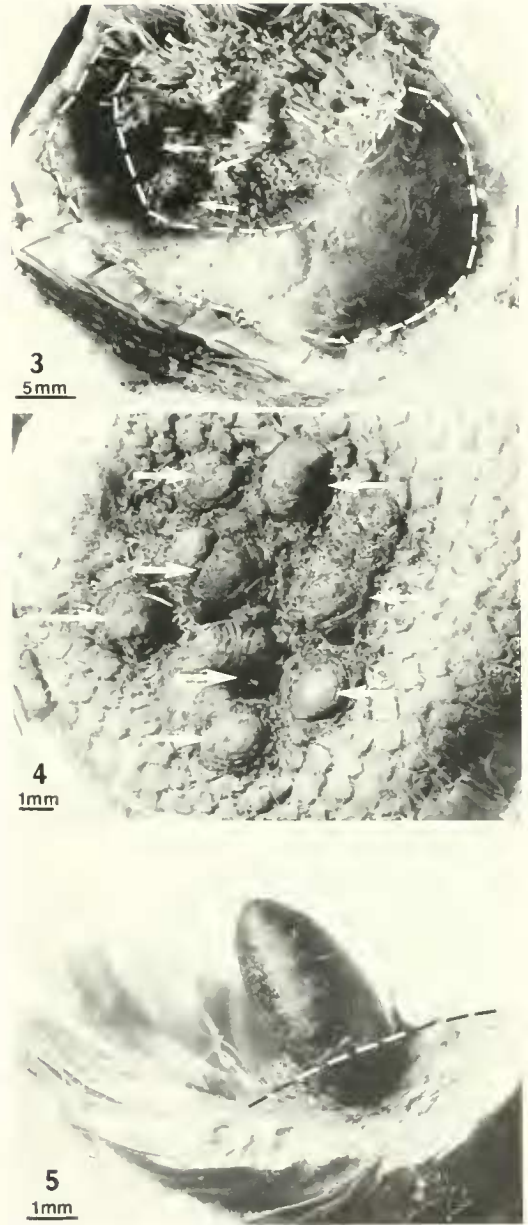


Fig. 3. Face view of dissected *C. proteanum* capitulum showing peripheral feeding path of *R. mucidella* (dotted-line), arrows show tops of centrally located *P. gentilis* puparia.

Fig. 4. Face view of receptacle of *C. californicum* pitted with *P. gentilis* cups formed by third instars.

Fig. 5. Cross-section of receptacle of *C. californicum* with *P. gentilis* puparium cupped in feeding cavity, dotted line denotes receptacle surface.

Table 2. *Cirsium californicum* capitula dissected ($n = 107$) containing late 3rd instar larvae or puparia, and the percentage of infested capitula with receptacle scoring by larvae.

	Infestation Class: No. 3rd Instar Larvae or Pupana per Capitulum						
	1	2	3	4	5	6	7
No. of capitula per class	32	27	23	8	4	3	2
No. (%) of capitula per class with receptacle scored	2 (6)	4 (15)	15 (65)	5 (62)	3 (75)	3 (100)	2 (100)

of spatial evasion was first recognized by Zwölfer (1979) for thistle-feeding tephritids in Europe, where he suggested it mitigated the effects of interspecific competition.

In contrast to *P. gentilis*, *O. occidentalis* and *R. mucidella* typically feed on the peripheral achenes (Figs. 2, 3). The value of this avoidance behavior was illustrated by dissection of a capitulum in which a *P. gentilis* larva had pupariated angled ca. 45° from a normal position perpendicular to the receptacle. The adult emerged abnormally towards the side of the capitulum, crossing the path of a *R. mucidella* larva which ate through it, leaving the head and abdomen behind!

Third instar feeding.—Dissection of infested *C. californicum* capitula also led to the discovery that if three or more *P. gentilis* third instar larvae were present in a capitulum, at least one had scored the upper receptacle centrally. In all capitula dissected, this receptacle feeding formed uniform cup-like depressions, 1.6 ± 0.09 ($\bar{x} \pm \text{S.E.}$) mm wide and 1–2 mm deep ($n = 35$) (Figs. 4, 5). The uniform depth and width of these depressions suggested a specialized function as sources of sap upon which the older larvae fed at higher larval densities. The mouthparts of the third instar, including the newly discovered “median oral lobe,” show modification for such liquid food uptake (Headrick and Goeden 1990). Fluid feeding by larvae of Tephritidae in galls, capitula, and other plant parts may be underappreciated in its importance and occurrence.

Romstöck (1987) reported that larvae of *Tephritis conura* Loew induced a callus while

feeding in the receptacle of *Cirsium heterophyllum* (L.) Hill. This structure then acted as a “sink” to maintain the nutrient flow to the head, much like a gall (Zwölfer 1985). That tephritid galls act as metabolic sinks in capitula of knapweeds (Subtribe Centaurinae), close relatives of *Cirsium* thistles (Subtribe Carduinae) was well demonstrated experimentally by Harris (1980). Thus, *T. conura* larvae similarly were found to induce and use callus formation to extend their resource limits, because the immature capitulum *per se* was a finite resource that did not contain enough nutrients to support completion of larval development. With *P. gentilis*, there was no induction of callus tissue or a gall, probably because receptacle scoring occurs after the meristematic stage and tissue differentiation (Harris 1980, 1989). Larval feeding apparently involves the slow, continual erosion and re-wounding of the upper receptacle during feeding-cavity formation to insure continued sap flow. In this manner, immature closed capitula of limited biomass can sustain several *P. gentilis* larvae.

This feeding mode is distinct from the receptacle feeding exhibited by species of *Cirsium*-head-infesting tephritids in Europe (Zwölfer 1988, Harris 1989) and elsewhere in North America (Steck 1984). As described by Steck (1984), *Chaetostomella undosa* (Coquillett) larvae bored into and fed on the receptacle tissues during all three instars. When larval densities were high, and after the receptacle was consumed, they mined downwards into the peduncle and stem. The scheme of Harris (1989) limits

Table 2. Extended.

Infestation Class: No. 3rd Instar Larvae or Puparia per Capitulum				
8	9	10	11	12
1	3	1	0	2
1 (100)	3 (100)	1 (100)	—	2 (100)

receptacle feeding by non-gall formers to immature "buds," but *C. undosa* continues to mine the receptacle through floret and achene growth stages (Steck 1984). *Paracantha gentilis* co-existed with *C. undosa* and was the dominant phytophage in *Cirsium capitula* sampled by Steck (1984). No other species of non-gall-forming, ovule or soft achene-feeding Tephritidae has yet been reported to feed on the ovules and then score the receptacle in the manner of *P. gentilis*, cf. Tauber and Toschi (1965), Stegmaier (1967), Cavender and Goeden (1982, 1984), Lamp and McCarty (1982), Goeden (1987), and Goeden et al. (1987). These data also clearly demonstrate that tephritids associated with Nearctic *Cirsium* spp. show novel feeding habits distinct from Palearctic tephritids (Zwölfer 1988, Harris 1989).

This change in third instar feeding patterns was analyzed in capitula containing only *P. gentilis* larvae. The average number of third instars found in 107 infested capitula was 3.3 ± 0.3 (range, 1–12). The receptacle diameter (used as an index of available resources) was highly correlated with the number of achenes per capitulum (corr. coeff. = 0.851, $P = 0.001$, $n = 25$). However, there was no significant correlation between the diameter of the receptacle and the number of larvae in a given capitulum, so the size of a capitulum did not limit infestation density.

Dissections showed, instead, that the age of the third instar as well as larval density determined the feeding mode. When capitula contained fewer than three third instar larvae, they usually fed centrally on the

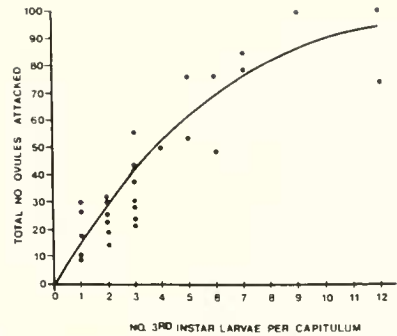


Fig. 6. Relationship of total ovules attacked per capitulum and *P. gentilis* third instar density.

ovules and pupariated without scoring the receptacle (Table 2). A change in third instar feeding behavior took place in capitula with three or more individuals; instead of continuing to feed on the ovules, at least one, possibly the smallest and/or the youngest, third instar(s) scored the receptacle. This occurred in 65% of all the capitula dissected containing three third instars. All capitula containing six or more (up to 12) third instar larvae had scored receptacles (Table 2).

Zwölfer (1985) noted that the number of achenes (ovules) attacked was a more precise measurement of resource utilization than the percentage of capitula attacked. However, in capitula of *C. californicum* containing from three to 12 puparia, complete consumption of the ovules never was detected. The number of ovules attacked per larva decreased as densities rose (Fig. 6). This decrease was not due to a depletion of resources (ovules), intraspecific competition and larval starvation, as suggested for *P. culta* (Wiedemann) by Lamp and McCarty (1982). Instead, this reflected a new resource, i.e. the receptacle, being used along with the central ovules by the younger third instars. Therefore, the precision of the statistic for resource utilization is dependent on the feeding strategy of the species of Tephritidae involved.

Ecological significance.—By not consuming all the achenes in a capitulum, *P. gentilis* followed the strategy of "evasion," as de-

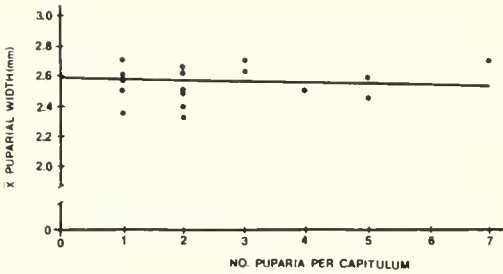


Fig. 7. Relationship of mean puparial width of *P. gentilis* per capitulum of *C. californicum* to pupal density (corr. coeff. = 0.059, n.s.).

finied by Zwölfer (1979) for thistle-head-infesting tephritids. However, the strategy of a "non-interactive grazing system" in which the phytophages merely consume a surplus of seeds produced (Zwölfer 1979) does not apply to *P. gentilis* in *C. proteanum* capitula. At the Sawmill Mt. location, where the guild was complete, i.e. at least three insect species infested the capitula, total consumption of achenes occurred in 60% of 50 infested capitula dissected. *Paracantha gentilis* had the advantage in this system by its optional use of an evasion strategy, i.e. being able to augment ovule-feeding with another, replenishable resource—plant sap from the receptacle. In this manner, *P. gentilis* avoided most competition from other guild members as well as among its siblings at high densities.

Several parameters were measured on adults reared from puparia dissected from capitula containing one to 12 individuals to determine if there were any effects of upper receptacle-moderated sap-feeding on puparial and adult sizes. No significant difference in puparial widths was found among individuals in capitula containing low and high fly densities (Fig. 7). Percentage adult emergence showed no differences among capitula containing different numbers of puparia, i.e. 54 of 58 (91.8%) adults emerged from unparasitized puparia. Head widths, hind tibial lengths and oviscapae lengths of adult females also showed no significant correlation among flies that emerged from

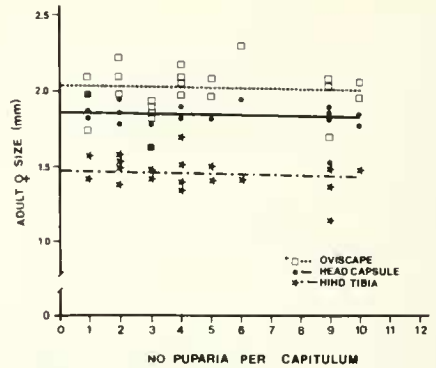


Fig. 8. Relationship of three *P. gentilis* adult female measurements (max. head width, hind tibia length, oviscapae length) to pupal *P. gentilis* density per capitulum (corr. coeff. = 0.181, 0.154, 0.033, respectively, n.s., $n = 27$).

capitula containing low or high numbers of puparia (Fig. 8).

CONCLUSION

The trophic strategy involving early-aggregated attack in capitula by Tephritidae, as now studied with both Palearctic and Nearctic species, shows three types of adaptations to extend and partition a finite resource, the capitulum. These adaptations involve tephritids that induce galls in the immature capitula (Zwölfer 1985); callus-forming tephritids (Romstöck 1987); and as reported in the present study, a receptacle-scoring tephritid that induces no plant tissue growth, and thus directly feeds on assimilates channelled to the immature capitulum.

Is *Paracantha gentilis* evolving towards gall formation? According to Zwölfer (1983), the most evolutionarily advanced insect-thistle capitulum relationship is gall formation. This implies an intimate, long evolved relationship between insect and host plant. However, Zwölfer (1988) noted that tephritid species maintained their trophic preadaptations during host transfer, i.e. gall-formers induced galls on any new host. By this interpretation, *P. gentilis* was preadapted to feed in *Cirsium* capitula without inducing tissue proliferation. But, is the change

to receptacle feeding by third instars also a pre-adapted feeding response to infestation densities, or an evolved adaptation to reduce inter- and intraspecific competition within thistle capitula? If it is the latter, *P. gentilis* may further evolve into a gall former. North American *Cirsium* thistles lack gall-forming insect associations (Goeden and Ricker 1987b). Supplementing findings by Zwölfer (1985, 1988) and Romstöck (1987), we suggest that receptacle scoring by *P. gentilis* represents just one end of a spectrum of feeding strategies evolved by thistle-head infesting tephritids, i.e. a new category of an early aggregated attacker that makes use of an immature capitulum in a unique manner to support its larval development without recourse to gall or callus tissue formation. In this manner the infested, closed, immature capitulum itself acts like a gall, offering the larvae a food source and constant micro-environment protected from desiccation, predation, and most parasitoids (Headrick and Goeden 1989b).

The "feeding niche" of *P. gentilis* in thistle capitula is thus novel by European criteria (Zwölfer 1988, Harris 1989). Therefore, it and associated herbivores exemplify the failure of phytophage communities to converge in structure despite similar resources on different continents, as demonstrated with bracken (*Pteridium aquilinum* (L.) Kuhn.) and its herbivores in England, New Mexico, and South Africa by Lawton (1976, 1982) and Compton et al. (1989).

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